STUDIES IN THE CLEOMACEAE I. ON THE SEPARATE RECOGNITION OF CAPPARACEAE, CLEOMACEAE, AND BRASSICACEAE[1]

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ABSTRACT

Molecular data support the recognition of three monophyletic families, Capparaceae s. str., Cleomaceae, and Brassicaceae, instead of an all-encompassing Brassicaceae or a paraphyletic Capparaceae s.l. This view is reinforced with many figures showing two basic and ubiquitous differences in cleomoid seed structure. First, the more or less strongly incurved seed, varying from reniform to horseshoe-shaped, coiled or conduplicate, uniformly and in all species, results in a deep invagination of the testa (the cleft) projecting into the interval between the two ends, or claws, of the embryo (this invagination is absent or rarely reduced and atavistic in Brassicaceae, and infrequent in Capparaceae s. str., i.e., in some *Capparis* L. species and *Crateva* L., sister genus to all remaining Capparaceae s. str.). Second, the uniformly semicylindric, strictly incumbent cotyledons are small and narrow, but are never foliaceous and interfolded, circinate or convoluted, or massive and thick, as in the often accumbent, rarely incumbent Capparaceae, or as variable as in Brassicaceae. An illustrated glossary of Cleomaceae seed morphology, as well as depictions of Capparaceae, Cleomaceae, and Brassicaceae seeds and their sectional views, and a key to all three families, are included.

Key words: Brassicaceae s. str., Brassicales, Capparaceae s. str., Cleomaceae, embryo morphology, familial realignments, seed structure.

Brassicaceae and Capparaceae s.l. have long been thought to be closely related families, a relationship that is supported by morphological and chemical data (Fig. 1; e.g., Iltis, 1957; Rodman et al., 1993, 1994, 1996; Rollins, 1993; Hall et al., 2002). Until recently, the approximately 45 genera and 800 species of the pantropical family Capparaceae s.l. have been classified into two major subfamilies, Capparoideae and Cleomoideae (Pax & Hoffmann, 1936; Melchior, 1964). However, molecular and morphological phylogenetic analyses of the family and relatives reveal that Capparaceae as traditionally circumscribed are paraphyletic, with the larger, mostly temperate family Brassicaceae embedded within it (Rodman et al., 1993, 1994, 1996; Judd et al., 1994; Hall et al., 2002, 2004). Chloroplast sequence data strongly support the monophyly of the three lineages: Brassicaceae s. str., Capparaceae subfam. Capparoideae, and Capparaceae subfam. Cleomoideae, with strong support for a sister relationship of Cleomoideae to Brassicaceae (Hall et al., 2002, 2004; Hall, 2008).

Thus, phylogenetic relationships inferred from chloroplast sequence information (*ndhF*, *trnL-trnF*, *matK*, and *rbcL*) and the criterion of monophyly permit three alternatives for familial recognition (Fig. 1): (A) three families, Brassicaceae s. str., Cleomaceae, and Capparaceae s. str.; (B) two families, Brassicaceae (including Brassicaceae s. str. and subfamily Cleomoideae) and Capparaceae (represented only by subfamily Capparoideae); and (C) one single family, Brassicaceae s.l. (Angiosperm Phylogeny Group, 1998, 2003; including Brassicaceae s. str. and Capparaceae s.l. and subfamily Cleomoideae; see Judd et al., 1994 for arguments on the priority of the name Brassicaceae over Capparaceae). In more recent literature, two of these alternatives are prevalent. Some authors merge all three into one, all-inclusive Brassicaceae (Angiosperm Phylogeny Group, 1998, 2003; Judd et al., 1994, 2007), whereas

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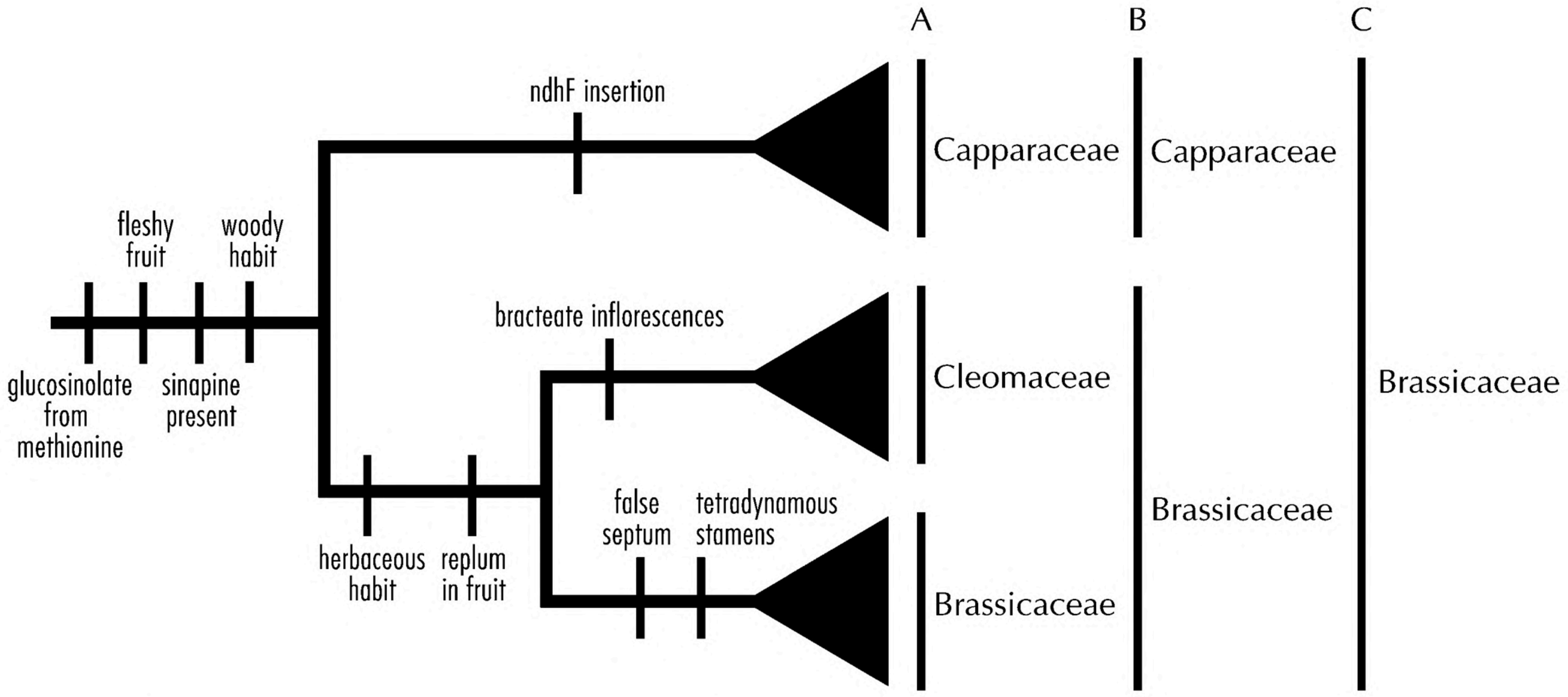

Figure 1. Three scenarios (cf. family names at right) for family recognition in the Brassicaceae, Cleomaceae, and Capparaceae clade consistent with molecular data. Distinguishing morphological characters are placed to represent synapomorphies (shared derived character states). Adapted from Hall et al. (2002: 1840).

others recognize three separate families (Hall et al., 2002; Simpson, 2006; Heywood et al., 2007), the concept now adopted by the Angiosperm Phylogeny Group (2009). Here, we argue that it would be much less disruptive and practical to recognize three monophyletic families.

In addition to the criterion of monophyly, there are other considerations to take into account when establishing familial boundaries. These factors include stability, ease of identification, and level of support for monophyly (Backlund & Bremer, 1998). The Brassicaceae s. str. are a cohesive and easily identifiable family. In fact, in light of the distinctive morphological features of its members, Brassicaceae have been one of the few families to be recognized as such throughout recorded history (Rollins, 1993). The Cleomaceae are also readily identifiable (see key below). Recent phylogenetic studies are making Capparaceae s. str. more cohesive, with many of the morphologically inconsistent taxa having been removed (e.g., *Setchellanthus* Brandegee to its own family Setchellanthaceae: Carlquist & Miller, 1999; Iltis, 1999; Karol et al., 1999; Tobe et al., 1999; Tomb, 1999; *Physena* Noronha ex Thouars to its own family Physenaceae: Takhtajan, 1985; *Stixis* Lour. [including *Roydsia* Roxb.], *Tirania* Pierre, *Neothorelia* Gagnep., and *Forchhammeria* Liebm. to one or more small families, the classification yet to be worked out: Kers, 2003; Hall et al., 2004). In addition, the elevation of the two subfamilies of Capparaceae to familial status had been suggested and accepted some 40 years ago by previous taxonomists (Airy Shaw, 1965; Hutchinson, 1967).

Although there are many clear morphological synapomorphies for Brassicaceae and Cleomaceae (Figs. 1, 2I–Z, 3; key to the three families), those for Capparaceae are more elusive (Figs. 1, 2A–H). Despite the lack of clear morphological synapomorphies, Capparaceae can easily be distinguished from Brassicaceae and Cleomaceae (key below; Table 1) by

Table 1. Morphological comparison of Capparaceae, Cleomaceae, and Brassicaceae.

	Capparaceae s. str.	Cleomaceae	Brassicaceae s. str.
Habit	woody	herbaceous, rarely woody	herbaceous, rarely woody
Leaf structure	simple, occasionally compound	compound, rarely simple	simple, rarely compound
Fruit morphology	fleshy capsules or berries, indehiscent (usually) or dehiscent, rarely with a replum	dry capsules, dehiscent with a replum, very rarely indehiscent	dry siliques or silicles, dehiscent with a replum and false septum, rarely indehiscent, sometimes transverse-jointed
Arils	often present	sometimes present	rarely present
Seed shape	globose to ovoid, ellipsoid, or reniform, testa shallowly or not invaginated	mostly reniform to reniform-orbicular or horseshoe-shaped, testa deeply invaginated	various, commonly globose, ovoid, or oblong, often (somewhat) flattened, lacking a cleft or testa not deeply invaginated
Cotyledons	incumbent to accumbent	incumbent	incumbent, accumbent, conduplicate or spirally coiled

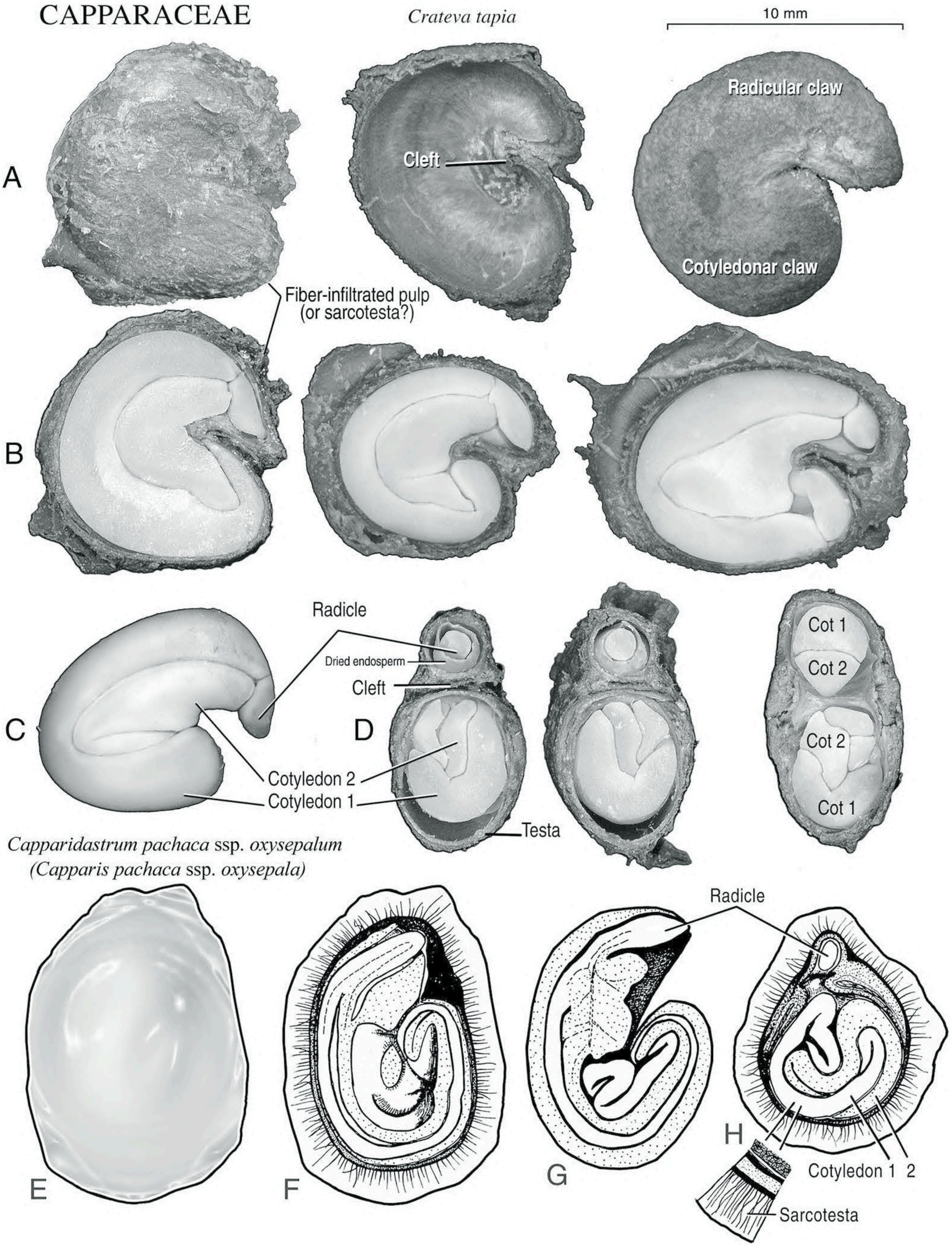

Figure 2. Seed morphology in Brassicales: configurations of embryo and testa. A–H. Seeds of New World Capparaceae. A–D. *Crateva tapia* L. (Nicaragua, Chontales, *Nee 28459* [WIS]). —A. Seeds, exterior views, surrounded by irregularly shaped, pulpy, densely hair-infiltrated sarcotestas. —B. Longitudinal sections of seeds (A, at left, and B, at left, views of the same seed), showing the very short, conical radicle sharply differentiated from the cotyledons by deep constrictions; the strongly asymmetrical connections of the two cotyledons to the radicle; and the greater length and thickness of the outer cotyledon, which obliquely embraces the inner and, at its tip, curves around and over the latter. —C. Whole embryo (views of the same seed as A and B at left and above), with testa removed. —D. Cross sections of seeds. D views at left and center represent the two halves of the same seed sectioned through the radicle and the near far ends of the convoluted cotyledons, to show the J-shaped cotyledon 1 obliquely embracing cotyledon 2. D view of seed at far right is sectioned through the base of the cotyledons just above the radicle, where only here they are shown to be, at least at the base, strictly incumbent. (Caption continued on next page.)

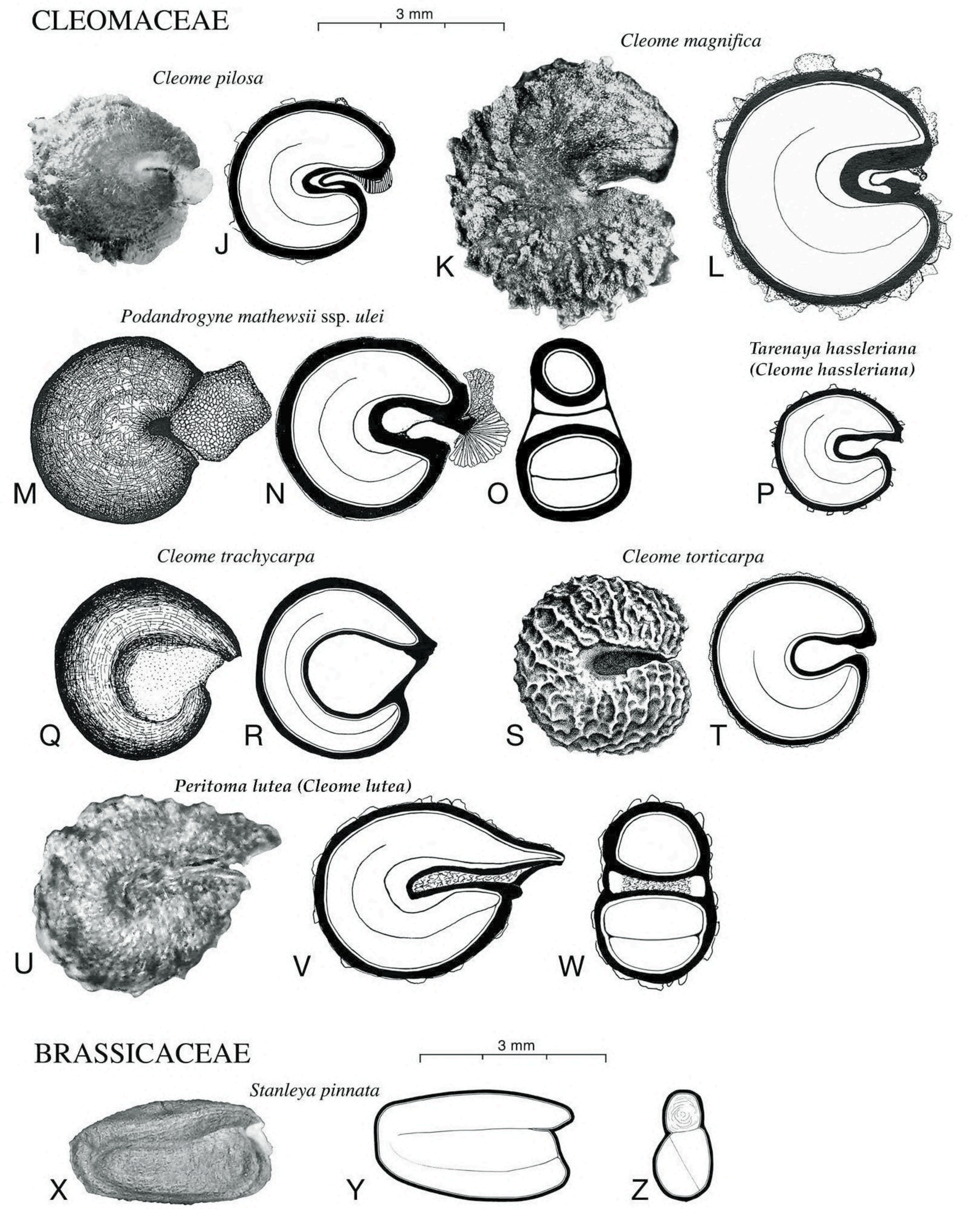

Figure 2. Continued. E–H. *Capparidastrum pachaca* (Kunth) Hutch. subsp. *oxysepalum* (C. Wright ex Radlk.) Iltis (Mexico, Oaxaca, *King 1479* [WIS], from Iltis, 1965: 60, cf. for detailed description; cf. also Cornejo & Iltis, 2008b). —E. Seed, exterior view, surrounded by a jellified, opaque, hair-infiltrated sarcotesta. —F. Longitudinal diagram of E. —G. Diagram of conduplicate embryo only. —H. Cross section of E, showing views as in F–H, with the two basally incumbent but distally convoluted cotyledons wrapped around each other and the radicle (hence the embryo conduplicate) and, as in F, the absence of a significant testa invagination between radicle and cotyledons. This is the usual condition in many species of Capparaceae (e.g., *Cynophalla flexuosa* (L.) J. Presl [= *Capparis flexuosa* (L.) L.]). I–W. Seeds of New World Cleomaceae. —I–L. *Cleome pilosa* Benth. (I, J) and *C. magnifica* Briq. (K, L). Both show the deep invagination of the testa forming the seed cleft and, into it, the secondary invagination of the cleft membrane, resulting in a small, internal cleft chamber and a short, open outer cleft. *Cleome pilosa* bears a small, funicular aril at the tip of the radicular claw, the probable precursor of that peculiar structure in *Podandrogyne* Ducke. —M–O. Seed of *P. mathewsii* (Briq.) Cochrane subsp. *ulei* (Briq.) Cochrane, a member of a speciose genus closely related to *Cleome*, characterized, inter alia, by arillate seeds semipersistent on the replum and presumably dispersed by ants (Iltis & Cochrane, 1989; Cochrane, 1997, 2011). P–T. (Caption continued on next page.)

the retention of a number of plesiomorphic characters, including woody habit, fleshy fruits with often arillate or sarcotestate seeds, and, rarely, compound trifoliolate leaves (e.g., *Crateva* L., some species of *Ritchiea* R. Br. ex G. Don, *Thylachium* Lour., and *Maerua* Forssk.). Although palmately compound leaves in *Crateva* have been suggested as a synapomorphy for Cleomaceae (Judd et al., 1994), the presence of this character state in *Crateva*, a genus that is sister to all other Capparaceae (Hall et al., 2002; Hall, 2008), contradicts this synapomorphy. In addition, compound leaves occur in the other closely related families in the order, Tovariaceae and Forchhammeriaceae nom. ined. (e.g., *Forchhammeria trifoliata* Radlk.).

The Cleomaceae differ from both Capparaceae and Brassicaceae by uniformly strongly curved, reniform or horseshoe-shaped to conduplicate seeds with an incurved embryo with always strictly incumbent cotyledons, in which its two ends are always separated by a deep invagination of the testa, the cleft (Fig. 2I–W; Sánchez-Acebo, 2005: 188–192, figs. 4–7; Iltis, Cochrane & Tucker, unpub.: figs. 1, 3). In most Capparaceae that have been studied (New World representatives), however, this testa invagination is usually shallow and obsolete, or simply consists of a very short, scalelike projection from inside the testa that does not intrude deeply into the embryo. Moreover, the embryos (but not the seeds) of Capparaceae are often sharply conduplicate, as if derived from reniform or conduplicate seeds in which the testa invagination has been deleted. Thus, these typically conduplicate embryos of Capparaceae sometimes appear straight (in species with elongate siliques) or spherical (in round berry fruits), but with the convoluted, often circinate and foliaceous cotyledons variously folded or wrapped around both each other and often around the radicle as well, in a complicated fashion (Fig. 2A–H; Eichler, 1865: tab. 64, 65; Iltis et al., 1996: 380, fig. 1D), thus often betraying their evolutionary origins in cleomoid-like seeds.

Crateva are of particular interest because the phylogenetic position of the genus as sister to all remaining Capparaceae may provide insight on putative primitive character states. Specifically, there are significant cleomoid characteristics of the *Crateva* seed that support the strongly curved, deeply invaginated reniform seed as a plesiomorphic character. Among the exceptions are the capparoid embryos inside of the cleomoid seeds of *Crateva* (e.g., *C. tapia* L.) that, strongly curved, from reniform to conduplicate, have a profound, wide to narrow invagination of the testa projecting deeply into the embryo, sometimes as deep as the seed's center or even beyond (Fig. 2A–D). Curiously, with the *Crateva* radicle-hypocotyl axis being conical and exceedingly short (in *C. tapia* only 1.5–2 mm; cf. Fig. 2B), and with its basally incumbent yet irregularly ill-fitted and somewhat unequal cotyledons filling more than nine tenths of the curvature of the testa, the tip of the seed invagination ends essentially in the center of the elongated cotyledons, unlike the situation in Cleomaceae, in which it touches the embryo near the base of the strictly incumbent, narrow cotyledons, and close to the transition to the elongated radicle-hypocotyl axis. Thus, the deeply invaginated, reniform seed of *Crateva* is a strong candidate as the plesiomorphic seed characteristic (Jacobs, 1960, 1964; Cornejo & Iltis, 2008a). Conversely, that its fat, irregularly incumbent cotyledons (Fig. 2A–D) do not lie horizontal and flat against each other as in Cleomaceae, but are variously and obliquely fitted one into the other, and with tips doubled and folded over each other and around the radicle as well, presages the typical, convoluted capparoid condition (Fig. 2E–H).

Eichler (1865: 239–242, 263–264, tab. 54–65) was evidently the first who appreciated these seed and embryo characteristics that distinguish Cleomaceae from Capparaceae. Within his all-inclusive Capparideae, he treated them as tribes distinguished by fruit type, cotyledons, and habit. Although these characters were not considered by Pax and Hoffmann (1936), Hutchinson (1967) emphasized the convoluted embryos and cotyledons of Capparaceae, which, except for the few but generally excellent seed illustrations in Eichler (e.g., 1865: tab. 64, figs. II 16, III 16), have rarely been adequately illustrated (Fig. 2A–H; Iltis, 1965: 60, fig. 2A–C; Iltis et al., 1996: 380, fig. 1D; Franceshini & Tressens, 2004: 213, figs. 4D–K, 5C; Iltis, Cochrane & Tucker, unpub.:

Figure 2. Continued. Seeds of *Tarenaya* Raf. (= *Cleome* sect. *Tarenaya* (Raf.) Iltis) revealing the large, empty, spherical cleft chamber closed at the cleft mouth, this evidently an adaptation for aquatic dispersal. —P. Seed of *T. hassleriana* (Chodat) Iltis (= *C. hassleriana* Chodat), a river margin and swamp species, commonly cultivated as *C. spinosa* Jacq. —Q, R. Seed of *C. trachycarpa* Klotzsch ex Eichler (from Iltis, 1967), another swamp species. —S, T. Seed of *C. torticarpa* Iltis & T. Ruíz (from Iltis & Ruiz-Zapata, 1997). —U–W. Seed of *Peritoma* DC. *Peritoma lutea* (Hook.) Raf. (= *C. lutea* Hook.), a species of arid grasslands and sands with conduplicate seeds and deep, narrow, tissue-filled seed clefts (from Iltis, 1950). X–Z. Seeds of Brassicaceae s. str.: *Stanleya pinnata* (Pursh) Britton (Ventura Co., California, *Bouquet s.n.* [WIS]), with a conduplicate-oblique embryo and a very short, nearly obsolete testa invagination between the radicle and inner cotyledon. Drawings by K. Elliot and H. H. Iltis (WIS).

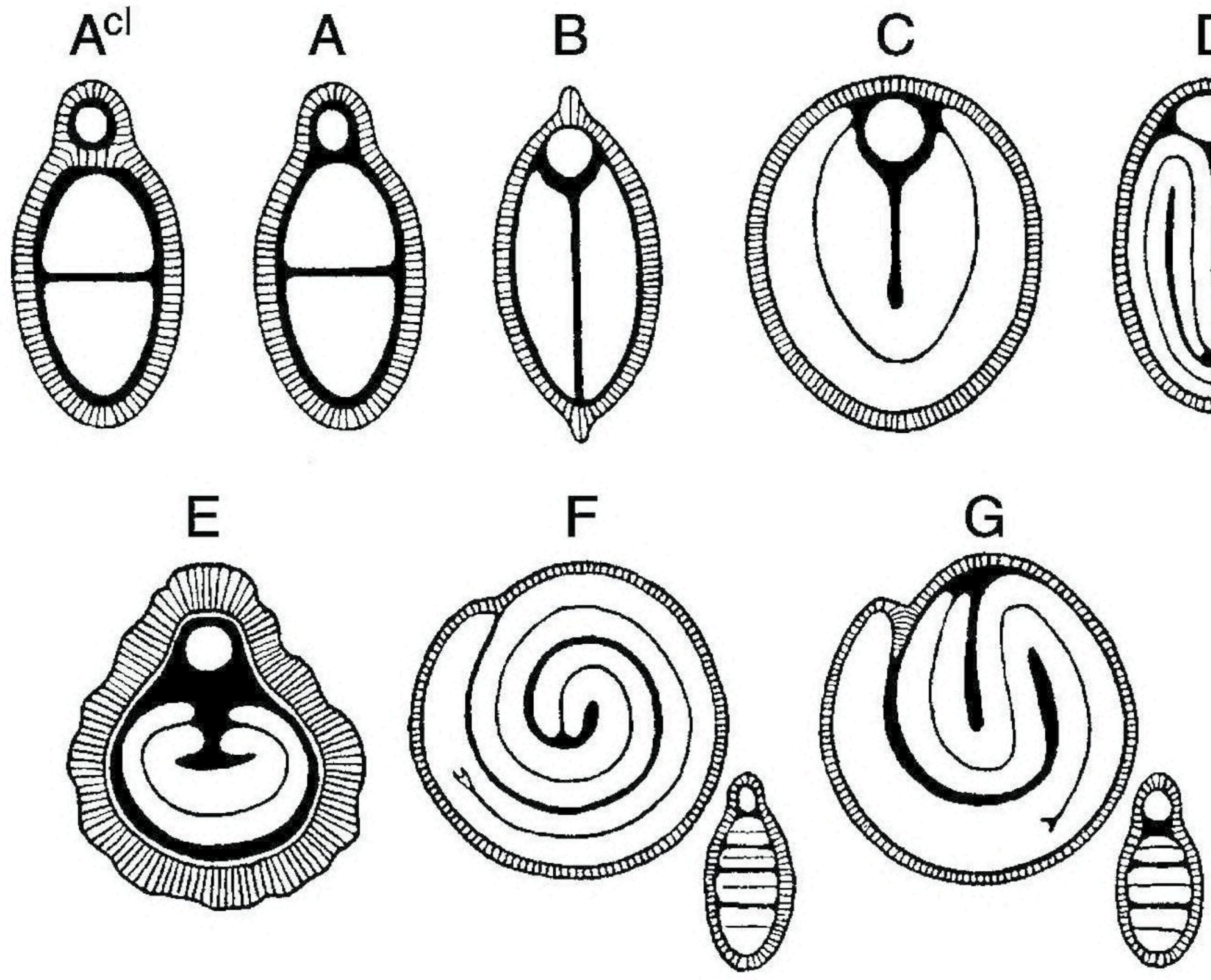

Figure 3. Seed morphology in Brassicales: configurations of embryo and testa. Cleomaceae (A$^{\mathrm{cl}}$) and Brassicaceae (A–G), with testa indicated by short parallel lines. —A$^{\mathrm{cl}}$. Cleomaceae, all species have uniformly incumbent cotyledons, e.g., *Tarenaya hassleriana* (Chodat) Iltis (= *Cleome hassleriana* Chodat) (cf. Fig. 2I–W, Cleomaceae; Fig. 2P, *T. hassleriana*; Iltis, Cochrane & Tucker, unpub.). A–G. Brassicaceae, showing the great diversity of embryo and testa configurations in this family, cf. Fig. 2X–Z. —A. *Sisymbrium strictissimum* L., with incumbent cotyledons. —B. *Cheiranthus cheiri* L., accumbent cotyledons. —C. *Brassica nigra* (L.) W. D. J. Koch, conduplicate cotyledons. —D. *Chamira circaeoides* (L. f.) Zahlbr., doubly conduplicate cotyledons. —E. *Calepina irregularis* (Asso) Thell., cross-folded cotyledons. —F. *Bunias erucago* L., spirolobous cotyledons. —G. *Heliophila pusilla* L. f., double cross-folded cotyledons. A$^{\mathrm{cl}}$, from Iltis original drawing; A–G, adapted from diagrams in Melchior (1964: 184).

fig. 3). Clearly, much work remains to be done on utilizing these valuable yet cryptic, poorly understood, and variable characters of embryo and seed.

The mostly highly specialized seeds of Brassicaceae show remarkable variability in their cotyledonar and radicular configurations (Fig. 3A–G), yet some derived genera, like those of Cleomaceae (Fig. 3A$^{\mathrm{cl}}$), have a simple and incumbent or oblique conduplicate embryo (e.g., *Stanleya* Nutt., Fig. 2X–Z), in which the invagination of the testa in between the cotyledons and radicle is all but obsolete or very short (Fig. 2Y).

In conclusion, subsuming Capparaceae s.l., or even just the Cleomaceae, within an expanded Brassicaceae would obscure the many clear morphological characters that leave Brassicaceae a vast, yet practical, cohesive, and highly specialized family. The Cleomaceae constitute a distinct entity that is sister to Brassicaceae. Capparaceae, a more diverse family than Cleomaceae, lie sister to Brassicaceae plus Cleomaceae. This arrangement suggests that all three of these monophyletic clades should be recognized as independent families, lending powerful support to Airy Shaw's (1965: 256) conclusion that "...the recognition of the Cleomaceae is a logical necessity."

Key to the Capparaceae, Cleomaceae, and Brassicaceae

The following taxonomic key and family comparisons use mostly easily determined and visible characters, relying often on seed sectional views (Figs. 2–4), but do not delve into technical anatomical details of testa, exocarp or endocarp, or the fully mature fruit wall, which, while undoubtedly useful, cannot be dealt with easily by the closet taxonomist, who is faced with the almost hopeless task of resuscitating dried-out, squashed, fleshy fruits and juicy seeds glued-down together permanently onto herbarium sheets (cf. Kers, 2003, for references).

1a. Fruits with a false septum (rarely lacking, e.g., in *Pringlea* T. Anderson ex Hook. f.); stamens 6 (also 4 or 2 in *Lepidium* L., 10 to 16 in *Megacarpaea* DC.), most often tetradynamous (4 long, 2 short); seeds lacking a cleft or deep testa invagination between radicle and cotyledons; seeds small (0.5–2 mm); leaves not pulvinate .... Brassicaceae

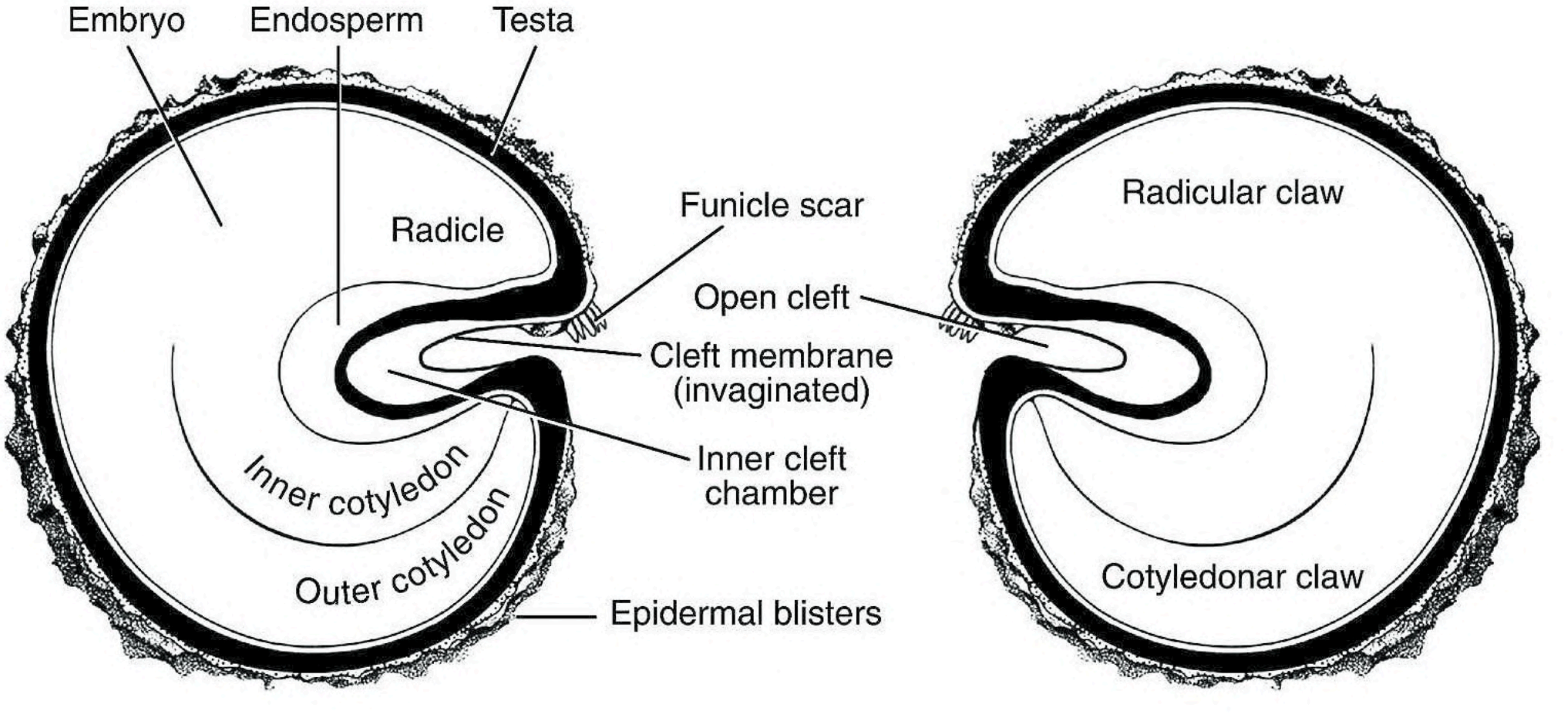

Figure 4. Cleomoid seed morphology: an illustrated glossary, based on *Cleome magnifica* Briq., as an example.

1b. Fruits lacking a false septum; stamens 1 to 250, not tetradynamous; seeds with or without a cleft or deep testa invagination between cotyledons and radicle; seeds small to large (0.5–30 mm); leaves often with pulvinate petioles 2

2a. Herbs, subshrubs, or rarely treelets; flowers often bracteate; leaves palmately compound, rarely unifoliolate or simple; fruits typically dry; seeds dry, small (0.5–4 mm), from either reniform or horseshoe-shaped to coiled or conduplicate, with the testa deeply invaginated between radicle and the narrow, semi-cylindric, always incumbent cotyledons, the radicle-hypocotyl elongate .... Cleomaceae

2b. Trees or shrubs, rarely woody vines; flowers not noticeably bracteate; leaves simple or unifoliolate, rarely trifoliolate (*Crateva*); fruits fleshy and/or pulpy; seeds often surrounded by an aril or sarcotesta, large (5–30 mm), round to elongate, less often reniform or conduplicate (*Crateva*, some *Capparis* L. species), the testa often shallowly or not at all invaginated; cotyledons often foliaceous and green, usually convoluted or circinate, or cross-folded with each other, sometimes white and greatly thickened, mostly incumbent to accumbent, the radicle-hypocotyl axis short and conical .... Capparaceae

COMPARATIVE DESCRIPTIONS OF BRASSICACEAE, CLEOMACEAE, AND CAPPARACEAE

Brassicaceae Burnett, Outl. Bot. 854, 1093, 1123. 1835, nom. cons. (cf. ICBN, App. IIB; McNeill et al., 2006: 140) TYPE: *Brassica* L.

Plants annual, biennial, to perennial herbs, rarely shrubby and woody; indument diverse, the hairs often malpighian, branched or stellate; mostly in cold to warm, often xeric temperate climates. *Leaves* simple, sessile, alternate, rarely opposite, sometimes pinnately dissected, lacking both stipules and pulvinus. *Flowers* usually in dense bractless racemes, generally actinomorphic and with small, white, yellow, or purple petals; stamens nearly uniformly 6 and tetradynamous, never forming an androgynophore; ovaries and fruits usually sessile, in a few genera (e.g., *Romanschulzia* O. E. Schulz, *Stanleya*) borne on a slender gynophore. *Fruits* dry elongate siliques to short and round capsules or silicles, variable in structure and dehiscence, the valves usually deciduous from a persistent replum that encircles a thin, translucent partition (false septum) dividing the fruit into 2 locules, or the valves (or parts thereof) persisting around a seed and falling as one unit, or seeds falling freely or permanently enclosed in parts of the fruit wall. *Seeds* (Figs. 2X–Z, 3A–G) small, mostly 0.5–2 mm diam.; testa smooth or variously ornamented, in longitudinal section usually not invaginated between cotyledons and radicle; *embryo* (Figs. 2X–Z, 3A–G) basically incumbent or accumbent (these two types nearly equally distributed in the family), variable, with the small, white cotyledons more often in diverse configurations, commonly lying against the radicle; *germination* always epigeal.

(For recent comprehensive references on the Brassicaceae, see Appel & Al-Shehbaz, 2002; Koch et al., 2003; Al-Shehbaz et al., 2006; Koch & Mummenhoff, 2006.)

Cleomaceae Horan., Prim. Lin. Syst. Nat. 92. 1834. [Isonym: Cleomaceae Airy Shaw, Kew Bull. 18(2): 256. 1965.] TYPE: *Cleome* L.

Plants annual or perennial herbs, often giant herbs or subshrubs, rarely woody shrubs to treelets; indument various, the hairs unicellular, uniseriate; mostly warm-temperate to tropical, arid desert or grasslands to humid, forested environments. *Leaves* alternate, petiolate and palmately compound, 3- to 11-foliolate, rarely sessile and/or unifoliolate (particularly in specialized taxa), thin and deciduous, rarely with minute, marcescent stipules, sometimes with stipular but hair-derived thorns, pulvinate or epulvinate, entire or minutely serrulate. *Flowers* in bracteate or less often ebracteate racemes, or rarely singly in the axils of leaves, zygomorphic to actinomorphic, 4-merous, often pink to purple, or yellow to white or dull greenish, generally day-, evening-, or night-bloomers; stamens 6 to 27(to 110) or by sterilization of the basic 6 reduced to 4, 2, or 1 fertile and 1 to 5 staminodes (or 6 staminodes, i.e., functionally pistillate flowers in *Podandrogyne* Ducke), equal or of variable lengths, sometimes adnate for part of their length to the gynophore, forming an androgynophore; ovaries usually borne on a gynophore or sessile. *Fruits* dry, elongate to short, round capsules, the 2 valves freely dehiscing from a thin (thick in *Podandrogyne*), hooplike or framelike replum lacking a false septum; or, less often, dehiscing partway from the top but remaining basally fused to the replum and receptacle; or, very rarely (*Oxystylis* Torr. & Frém., *Wislizenia* Engelm.), valves each permanently enclosing and dehiscing with their 1 to 2(to 3) seeds. *Seeds* (Figs. 2I–W, $3A^{cl}$, 4) small, 0.5–3(–4) mm, strongly incurved, from either reniform or horseshoe-shaped to coiled or conduplicate, the two arms or claws of the seed free to the vertex (Fig. 4) to totally, or the basal half only, fused from without by an external cleft membrane, forming in longitudinal section a spherical and hollow, to narrow and wedgelike, or solid, closed, and obsolete, cleft chamber; seeds dry or, if carunculate, equipped with oil-filled cells or a white funicular aril and presumably dispersed by ants; testa dry, smooth to transverse-rugose or tubercled, glabrous or pubescent to variously ornamented. *Embryo* (Figs. 2I–W, $3A^{cl}$; Iltis, Cochrane & Tucker, unpub., figs. 1, 2) uniformly incumbent, with the semicylindric, narrow, straight cotyledons flat on top of each other, with the back of the inner cotyledon facing the radicle but separated from it by the deep cleft of the invaginating testa. *Germination* epigeal, the cotyledons in the seeds small, white, and not expanding into wide, green leaves. Seed viability variable, from short to many years.

Capparaceae Juss., Gen. Pl.: 62. 1789, nom. cons. (cf. ICBN, App. IIB; McNeill et al., 2006: 141). TYPE: *Capparis* L.

Plants shrubs to treelets to trees, sometimes scramblers, rarely (in the New World) lianas; indument various, the hairs unicellular, stellate or peltate; mostly subtropical to tropical, from dry to moist environments. *Leaves* usually alternate, distichous to spiral and clustered, simple or unifoliolate and pulvinate, petiolate to subsessile, rarely palmately trifoliolate (*Crateva*), often evergreen, entire. *Flowers* mostly in ebracteate, often corymbiform racemes or solitary in axils of leaves, actinomorphic to rarely zygomorphic, 4-merous, white or greenish to purplish white, usually night-blooming; stamens (1 to)8 to 250 (rarely 6), ± equal; ovaries mostly borne on gynophores, rarely sessile. *Fruits* either dehiscent, 2-carpellate, fleshy (rarely tardily dry), elongate capsules lacking a false septum or baccate with repla (the parietal placentae) mostly thin, the valves often tardily dehiscing or repla obscure or in indehiscent berries obsolete, lacking a false septum but sometimes with endocarp intrusions and then axile placentation. *Seeds* large, 5–15(–30) mm, spherical to ovoid or ellipsoid, straight or broadly incurved to reniform-conduplicate; testa smooth, thick and hard to very thin, slippery and easily removed, often covered by a fleshy-oily, funicular aril or by a hair-infiltrated sarcotesta (Fig. 2A–H), or immersed in the red, orange, or cream to white endocarp pulp; testa often shallowly or not at all invaginated into the embryo (deeply so in *Crateva*, *Capparis* spp.), the two claws of the seed not conjoined by distinct cleft membranes (Fig. 2A–H); *embryo* green to ivory-white, variable, mostly conduplicate, with cotyledons incumbent or accumbent, but often foliaceous, much enlarged and variously convoluted one inside the other and sometimes around the radicle (Fig. 2A–H); *germination* epigeal, the cotyledons often large, green, and leaflike, or sometimes ivory or white and very thick and food-storing, rarely quite unequal with one suppressed.

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